Dynamics of Soil Communities

A Summary of the papers presented at the third Colloquium of the Soil Zoology Committee at Braunschweig 5.–10. September 1966

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Analysing the title of this Colloquium: "Dynamics of soil communities", it seems important first to ask what is understood by "soil communities". Interpretations of the term community are manifold but they can be centered around two main conceptions. The first holds that the community is an assemblage of species populations which are to be described taxonomically and quantitatively. In this sense the term could perhaps better be substituted by biocenosis (Macfadyen 1957). The second view recognizes the intra- and interrelationships within and between the species populations and considers dynamic stability and organic unity as the essential properties of the community. It seems to me that both views are complementary in the study of species populations in nature just as morphology and physiology are complementary in the study of an individual organism.

PREREQUISITES FOR SOIL COMMUNITY STUDIES

Before a community can be described and its structure can be studied much technical and taxonomic work has to be done.
Technical work in the sense that the sampling procedure has to be elaborated and appropriate extraction techniques must be chosen. Both aspects are excellently surveyed in the Proceedings of our first Colloquium at Harpenden: Progress in Soil Zoology. It is pleasing that a new technique, the grease film extraction technique has now been added to the well known dessication and flotation techniques (Aucamp). It is, like the others, not 100 % efficient for extracting all groups of animals, but the impor-

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tant group of oribatid mites is extracted with exceptional efficiency. Advantages of the technique are its practicability in circumstances where other techniques cannot be used, its usefulness for extracting residues from funnel-operated samples and its utility for stored samples. For forest soil samples the technique seems to be less appropriate. In any case the new technique, which may in the future be the most efficient in certain circumstances, needs to be tested for other groups of microarthropods and for various soil types and to be compared with other methods.

In the field of soil biology tremendous gaps in our taxonomic knowledge exist. Though the study of the structure and the functioning of soil communities cannot be postponed till our taxonomic knowledge suffices, taxonomic work remains urgently needed. Since our last colloquium, the series Bestimmungsbücher zur Bodenfauna Europas was started and, up to now, 5 issues have been published and several others are in preparation. At the present colloquium also, several papers were concerned with taxonomic and biogeographical questions.

Knowledge of the geographical distribution of soil organisms is important for understanding their ecological requirements, their tolerances and their adaptations. In this respect the contributions of Alvarez on earthworms in Spain, Bhatti on enchytraeids in West-Pakistan, and Ryke and Loots on microarthropods in South Africa must be mentioned. These studies did not contribute only to knowledge of the geographical distribution of species, they also outlined their dependence on climate, soil type and vegetation, and their association with other species.

Ljungström has given us a description of the colonization of the Scandinavian peninsula by lumbricids in two phases and pointed to the role of man in the colonization history. It is exceptional that the origin of a soil fauna group can be traced so far. The historic influences on the development of biocenoses are in most cases completely unknown though they may be of utmost importance. A quite different approach to a better understanding of biogeographic patterns was presented by Athias-Henriot by introducing the concept "type of organisation". It maylead to a quite new taxonomic classification in the genus *Pergamasus*.

BIOTIC STRUCTURE OF SOIL COMMUNITIES

As we saw earlier, description of the soil communities can be made from several viewpoints. First may be considered what can be called the "biotic structure", that is to say the enumeration of the species of the commu-

nity and their characterization by certain parameters. In phytosociology such parameters are abundance, dominance, frequency, constancy and fidelity.

Description of the composition of the soil community expressed in quantitative terms encounters many more difficulties than the description of a plant community where the species present can be counted, weighed and measured by reference to the ground area which each of them covers. The soil community must be studied by analysing the biota contained in samples or by employing a special collection technique. The size of the samples has to be in a certain relation to the size of the organisms and the various groups require their own extraction techniques. A complete picture of a soil community has never yet been obtained and only by a thorough cooperation of specialists working in the same study area may it be expected to be attained. Even then it must be remembered that a community has essentially a dynamic character and that each repetition of the study will show differences caused by internal or external influences.

In a community, the distributional patterns of the various species populations are of great importance. Gérard's communication was concerned with the problem of characterizing statistically the horizontal distribution pattern of some oribatid populations. By analysing samples of different sizes and studying the parameters of the observed negative binomial distribution he reached conclusions on the most appropriate parameters for characterizing the rate of aggregation in the Oribatei considered: the species did not occur in separate islands but in diffuse zones of varying density, which may be related to parallel variations in environmental factors.

The mutual relation between communities may be expressed in several ways, e. g. correlation coefficient, index of affinity (Renkonen), quotient of similarity (Sørensen). From a matrix of such indices, by means of some kind of cluster analysis, mutually highly related communities may be discerned. Progress both on devising coefficients of association and on cluster analysis methods will give objective methods for delimiting community types. In most cases, however, the methods will not lead to new discoveries but confirm the opinions of field naturalists as remarked by Macfadyen.

In this colloquium Selga presented a biocenotic hierarchy in three mountain localities in Spain based on the degree of constancy of so called fundamental species of Collembola. She concluded that species that would

be classified as cosmopolitan and eurytope showed distinct ecological differences when their distribution over the biotopes within each of the mountain localities was considered.

A quite different approach to describing soil fauna communities is that of Volz. Based on the quantitative analysis of the macrofauna, the microarthropods and the thecamoebae, he discerned 5 physiognomic types of communities in the Southern Palatinate which to a certain extent indicated their dynamics. The analyses did not go down to a specific level but gave the biomass of important taxonomic groups. Each of these types could be subdivided by specification of the most appropriate groups. I feel that this approach may be very fruitful both in studies of the functional aspects of soil communities as a whole and for practical diagnostic purposes. Detailed studies on trophic relationships within the community and description of animal associations will require a more complete identification of the species concerned.

TROPHIC STRUCTURE OF SOIL COMMUNITIES

The system of trophic relationships between the members of the soil community may be called its trophic structure. The heterogeneous composition of the members of the soil community, their periodicities and their very incompletely known life and feeding habits makes an exact location of even the more abundant species in the food-chain a difficult task. Of course the soil community is not an independant entity. It is connected with other soil communities in manifold ways and also with the above-ground communities with which it forms the bigger forest-, meadow- or agricultural community. Though there are several examples of diagrams which outline roughly the food relations between the components of the community, the quantitative relations between various trophic levels are tentative.

In the quantitative approach to the trophic relationships within the soil community, numbers are quite insufficient. The greatly varying size of organisms makes them quite meaningless. To facilitate the conversion of animal numbers into biomass and biovolume, Edwards stated the average weights, dry matter contents and specific gravities of a great number of animal groups. He found a linear relationship between length and the cube roots of the weights. With the help of these graphs the live weights of animals can be estimated from measurements of their lengths. It may prove to be useful especially for smaller animals and for dealing with large numbers of animals.

Biomass and biovolume generally refer to populations as they are sampled in the field. In those cases where gut contents constitute a significant part of weight or volume as in earthworms, enchytraeids, diplopods and tipulids, this may handicap a fair estimation of the animal tissue and this is especially true where the gut contains considerable amounts of mineral substance. Bouché has worked this out with respect to three species of earthworms. Not only fresh weight, dry weight and density differed considerably, but also the contents of water, carbon and nitrogen. Though differences were to be expected it is useful to have exact observations by which it is possible to evaluate the inaccuracies arising from neglecting this circumstance.

Comparison of density and biomass curves of a population may bring to light special peculiarities of the population. In most cases a reproduction period is characterized by a strong increase in numbers but a very slight increase, if any, in biomass. At other times the changes are concurrent. Möller, however, found in an enchytraeid population concurrent increases in numbers and biomass at reproduction time and an opposite course during winter. The first deviation was caused by an exceptionally high growth rate of the species *Henlea perpusilla* and the second one by a *Marionina* species which reproduced at temperatures around the freezing point.

Having considered the term "community" we may continue the analysis of the theme of the colloquium and reflect on the term "dynamics". If we look for it in an encyclopaedia we see it defined as "the forces at work in any field". In our case this definition may be interpreted as forces working in soil communities (Internal Forces), forces working on soil communities (External Forces), and forces evoked by soil communities. The human influences on soil communities may be discerned as a special type of external forces.

INTERNAL FORCES IN SOIL COMMUNITIES

The forces within the soil communities which influence its development are the mutual relationships between the members. They can take forms like mating, brood-care, competition, predator-prey relations, symbiosis and stimulation or inhibition by excretions. This web of interrelationships together with abiotic influences decides the basic phenomena of population dynamics: natality and mortality. In several respects the soil population

seems an attractive field for population dynamics. However, the very incomplete basic information on most species and the great complexity of the biotic relationships are obstacles, the removal of which may take a long time.

In colonization and succession, mutual influences of biota are apparent. Minderman and Daniels described a technique by which the colonization of newly fallen leaves by microorganisms may be observed and measured. This and other studies show that it is practicable to investigate the succession of microorganisms on decomposing dead leaves but there may be advantages in studying this succession with the help of more homogeneous material inserted in the soil. Harding studied the colonization of cellophane inserts in forest soil and here the interrelationships of fungi, bacteria, nematodes and microarthropods seem evident. The whole successional process is highly influenced by seasonal meteorological conditions. By counting and measuring faecal pellets, the seasonal occurrence of certain stages of mite species could be demonstrated. Another colonization problem is that studied by Pugh: the origin and development of the root fungal flora. The seed coat flora plays a large role, especially in soils with relatively unfavourable conditions for fungal survival, in the colonization of the seedling roots, although the soil flora still exerts some influence. In the development of this rhizosphere community, competition between species is of great importance.

An interesting relationship between microorganisms was reported by Nagel - de Boois and Jansen. The discrepancy they found between mycelium content and hyphal growth in several types of forest floor is ascribed by them to differences in breakdown of mycelium in the soil. In mull soils, the mycelium content was lower but hyphal growth was about equal to that in mor soils. In mull, mycolytic organisms could be detected but in mor they were absent.

Microorganisms affect each other by their excretion products which may be stimulatory as well as inhibitory. Hagedorn demonstrated the dominant role of microorganisms in the production of vitamins in soil. Examples of inhibitory and stimulatory effects on mycorrhiza development are given by Meyer. *Penicillium* species, *Trichoderma viride* and *Alternaria tenuis* inhibit mycorrhiza development; vitamin and auxin-producing microorganisms sustain and stimulate it.

Trolldenier studied the proportion of rhizosphere and soil microbial populations and obtained higher ratios with the plate count technique than with fluorescence microscopy. The specific conditions in the rhizo-

sphere provide favourable circumstances for only part of the soil population, which develops abundantly. The alteration of the microbial population is characteristic of the rhizosphere effect much more than its quantitative enrichment.

The differences in microbial composition and activity in the rhizosphere of two associated plant species, *Chrysanthemum vulgare* and *Achillea millefolium*, were studied by Steubing. In the rhizosphere of *Achillea*, the numbers of bacteria, particularly those of *Azotobacter*, were greater, cellulose decomposition was quicker and mineralization as well as nitrogen fixation were higher than in the *Chrysanthemum* rhizosphere. Differences in composition of algal populations may have been responsible for different intensities of nitrogen fixation.

Vegetation produces the basic food for the soil community. It influences the soil community in a more specific way too. Palissa showed in his paper the effects of various plant extracts on Protozoa, Nematoda and Collembola. These influences seem of a very intricate nature. Differences occured with varying concentration and exposure times but also between sterile and non-sterile extracts as microbial activity may alter their effect.

A tentative study on the quantitative relation between microbivorous nematodes and bacteria was made by Banage and Visser in a virgin bush site in Uganda. Their conclusions suggest an enormous amount of potential food for the nematodes.

Satchell and Lowe studied food choice in earthworms and tried to explain why some types of leaf litter are preferred. They found preference broadly correlated with nitrogen content, soluble carbohydrate content and content of polyphenolic substances. Microbial activity may be of importance in the decrease of distasteful substances like tannins during weathering of oak litter.

Metabolism studies on soil populations receive increasing attention. Only by these is it possible to evaluate the relative importance of the various populations in the energy flow through the soil. By measuring ingestion and egestion, assimilation may be estimated by subtraction. The percentage of ingested food which is assimilated varies widely, depending on animal and food species and on the rate of food intake. In most litter-feeding macroarthropod species, feeding actively, not more than 5-10% of the ingested food is assimilated. It is the large percentage egested which makes these animals such an important agent in diminution of the litter, rendering it more accessible for attack by microorganisms. Assi-

milated food is partly respired, partly fixed in body tissue as growth. The proportion of these two parts also varies widely. In animals with a long lifetime, the energy content of the body tissue will be very low compared with the energy dissipated by respiration. In small terrestrial animals it is assumed that respiration is equivalent to 75-90% of assimilation, leaving only 10-25% for growth. In microorganisms with a quick turnover the proportions of energy stored up in body tissue may be much greater than this. Conversion of this dead body tissue may be greatly promoted by the activity of soil fauna.

Heal calculated the food intake, assimilation and growth in an interesting study on *Acanthamoeba* fed on *Saccharomyces cerevisiae*. Growth appeared to account for 37% of the food ingested and for about 58% of assimilation, a much higher value than the 10-25% mentioned above for small terrestrial invertebrates. This figure applies to optimal food and feeding circumstances and it may be different in a population in more natural circumstances with natural food.

A study on the respiration in a field population was made by Healey with *Onychiurus procampatus* in a moorland habitat. His estimates of mean biomass and annual energy utilisation point to a rather low significance of this group of the microarthropods. Though this type of study is rather scarce, available data suggest that microarthropods are rather low in importance relative to nematodes, enchytraeids and lumbricids in energy flow through the soil fauna.

EXTERNAL FORCES ON SOIL COMMUNITIES

Forces outside the soil community which influence it in its development and maintenance are edaphic and climatic factors. In addition to these, human activities may influence soil communities decisively.

In the first stages of a developing soil community, the combined action of edaphic and climatic factors select the appropriate species from the organisms which are available. These are autotrophic life forms, which, once settled, provide heterotrophs with an opportunity to start, although edaphic and climatic circumstances are of primary importance for them too. In later stages, the vegetation becomes an important factor, not only in forming vegetable debris as food, but also in reducing temperature and humidity extremes and in unlocking the soil by its root activity.

N o s e k gave a picture of the development of soil communities on limestone and on granitic rocks from the very beginning. The first colonization by groups resistant to extreme temperature and great dryness (Protozoa, Rotatoria, Tardigrada and Nematoda) is closely similar on both types of rocks but, in the initial soils, bacteria and fungal populations are quite different and with them the microarthropod populations. These initial stages of the soil community are rather simple in composition and their development into other more complicated ones is slow. Such soil communities are ideal for research on community metabolism: the number of species is limited and if the construction of a food web including all biota is possible anywhere it is here. It may be expected that studies in these environments will contribute much to our understanding of more complicated situations.

Studies on the natural development of the soil community are not restricted to weathering rocks. Newly reclaimed soils from the sea-bottom and artificial hills of soil and stones excavated in mining form good objects for study, as D u n g e r demonstrated. Succession, however, is quicker: the substrate is more appropriate as an environment for life, climatic conditions are less extreme and life forms of varying kinds are more readily available, especially after recultivation. Also in Dunger's paper the great importance of edaphic influences is pointed out. In dumps from pleistocene-tertiary brown coal exploitation the biomass of soil animals was from 10-100 times greater than in the acid tertiary sand in a nearby dump.

The influence of climatic factors on soil populations was studied by v a n R h e e (earthworms) and M o e l l e r (Collembola) by sampling these populations for several years. It is interesting to note that the same extremely severe winter, 1962-1963, had a similar detrimental effect on earthworms in an apple-orchard in the Netherlands; on springtails in marine seaweed wrack in Germany; and on oribatid mites in a forest soil in England (H a r d i n g). Whereas, however, the earthworm population did not succeed in recovering to the previous density level in the following years, the springtails reached maximum density after only two months and the oribatids, having declined to a minimum in April-May, reached a high density in August. This clearly demonstrates the different responses of soil animals in a wide area to the same macroclimatic influences. K o z l o v presented counts of microorganisms and their fluctuations in the dry steppe soils in the south-eastern Trans-Baikal area.

He illustrates the influence of soil moisture on microbe numbers and enzyme activities in soils with varying productivity.

An interesting study on the biological and chemical changes in soils which were transported to different climatic sites was made by Ahrens and by von Klopotek. They found a tendency for the soils to approach the level of the local soil which they ascribed partly to climatic factors and partly to edaphic factors. Though there were many questions that could not be answered, the general line of the results is promising and continuation along these lines may enlarge our insight into the interrelation between climate and soil in their influence on soil communities.

Another way to study the influence of climatic factors on the soil population is by measuring its total metabolic activity under changing conditions. A nice example of an investigation on these influences was given by Jager. He studied the influence of drying and remoistening, freezing and thawing on the activity of soil organisms in arable soil and the causes of the changes in activity. Remoistening after drying caused a sudden increase in CO_2 production which was explained mainly by the augmentation of easily decomposable products as a result of desiccation. Freezing followed by thawing, however, caused a decrease of CO_2 production which continued with repeated treatments but soon stabilized. It was explained by an increasing resistance to decomposition of the organic matter which could be reversed by drying. In soils with a higher organic matter content, freezing seemed also to increase the mineralisation of nitrogen. This may possibly be ascribed to killed soil organisms. Although in these experiments drying and freezing rates were studied which do not occur in the field, the same tendencies may be expected there.

Climatic influences may result in seasonal changes in distribution and activity. The great importance of water-content in tropical soils for the seasonal changes in the vertical distribution of microarthropods was shown by Belfield. By watering during the dry season to an extent of 7" of rain per month it was possible to maintain the distribution pattern with the highest density in the top layer. In control plots, desiccation of the top layer caused a downward movement of the animals resulting in an increasing density in the 2-6" layer.

The importance of water as a factor in the vertical distribution of fungi is demonstrated by Apinis. Increasing soil water-content and excess of water restricts or elimates a large number of terrestrial soil fungi. Low oxygen diffusion causing low oxydation-reduction potentials is pro-

bably the operative factor. In this study too, seasonal periodicity, caused mainly by change of soil temperature is apparent: growth frequency and number of species were much higher in summer than in winter.

A fine example of seasonal activity was worked out by Bocock and Heath. They showed that the millipede *Glomeris marginata* stops feeding in autumn at a soil temperature of about 6°C and migrates downwards to a depth below 5 cm. In spring, feeding and upward migration occur again at about the same temperature.

Another example of seasonal change in activity was given by Kneitz. In summer the red wood ant, *Formica polyctena*, is active in building and rearranging its vegetable hill, in autumn it excavates soil from its nest.

Diurnal rhythms in activity were studied by Heydemann in the epigeic fauna in coastal areas. Most species were active in the daytime and also the total number of active animals was greater by day. Nevertheless the total weight was smaller as many bigger species are active at night.

HUMAN INFLUENCES ON SOIL COMMUNITIES

Man influences soil communities in many ways. Changes in vegetation are in most cases the first effects of human presence. They are followed by more severe impacts when the land is cultivated and forest, pasture, orchards or arable land results. In most types of cultivation the soil communities deviate strongly from those under natural vegetation. Agricultural measures like tillage, manuring, crop rotation, etc. all have their influences and there are several well-analysed studies on the effect of these measures on soil life. Particularly in more recent years, application of pesticides has become an influence on soil life, the extent of which is barely known. In addition to the increasing extent of the application of insecticides, fungicides, nematicides and herbicides there is the increasing pollution of soil, water and air with the products of our civilization.

Studies on all these aspects of increasing influence of man on the soil community were represented in this colloquium.

Van den Berg and Ryke described the changes in mite fauna caused by cutting out indigenous forests and replanting the cleared areas with fast growing exotic *Pinus* species. It seemed that in this case the total mite population was reduced only by about 10%. Of the natural forest

species of Mesostigmata, 74 % were encountered in the pine plantations. The answering of many interesting questions which arise from this study will give us a better insight into the problems connected with the introduction of foreign species.

Ghilarov and Mamajev showed that man may interact successfully in the development of soil life in irrigated desert soils. They introduced mixed earthworm populations of which two species at least increased greatly after some years.

Striganova stated in her study of the soil coleopterous fauna in various forest types of the Northern Taiga that after the trees have been felled, the coleopterous fauna acquires a more southern character. So human activity seems to provide the route by which Coleoptera species extend their range northwards, - a clear example of indirect human influence on the geographical distribution of animals.

The development of soil fauna in dumps from brown coal mining was studied by Dunger. Twelve years after afforesting the dumps, the biomass of the macro- and megafauna was already of about the same size as the biomass in a neighbouring natural forest.

The effect of cultural measures on soil life is apparent from several studies. Atlavinytė et al. studied important soil fauna groups in various types of cultivation. They found the soil organisms in sod soil and in soil under perennials up to 10 times more abundant than in arable soil and in fallow soil.

The complicated effect of climate, cultural measures and varying crops on vertical distribution, population density and age class composition is demonstrated in the study of Anglade on three Symphyla species in cultivated soils. The ecological differences between the species resulted in different effects on each of them.

Van Rhee found pest control measures in orchards to be of utmost importance on earthworm populations. There are indications that copper oxychloride sprayings cause a decrease in reproduction and a gradual extinction of the population.

Effects of crop rotation and application of organic and mineral manure on soil microorganisms is shown by Jagnow. Different crop residues influenced *Azotobacter* populations differently. Organic manure often stimulated *Azotobacter* but straw compost inhibited its development. Mineral manure had only little effect.

In most agricultural practices, ploughing the soil is unavoidable and the bad effect with respect to soil fauna has to be accepted. The observa-

tions of Zicsi show that, by careful choice of operational time and implements, the damage can be reduced. Tillage by a shallow disc plough caused smaller losses of earthworms than tilling by a deep plough but, in addition, water-content was better conserved in the first case and this resulted in a quicker recovery of the population. Subsoil loosening evidently destroyed part of the earthworm population but, by maintaining a favourable water-content, a very great proportion of the earthworms remained active.
In many cases, however, tillage of the ground operated without any care for soil life may lead to very poor biological activity and thus to decline in structure and occurrence of erosion. This situation is often found in vineyard soils where frequent tillage is employed to prevent water-consuming weed growth, and where other necessary activities have also a detrimental effect on soil structure. Bosse showed that by such appropriate measures as fallowing, supplying of compost and mulching of straw and green weeds, recovery of the earthworm population is possible after some years and that soil structure may be improved considerably.

It is well known that the application of insecticides in the soil against soil pests, as well as on the crop, often results in the accumulation of great amounts of insecticides. Karg demonstrated the intricate effects of various insecticides on populations of Collembola and mites. By their selective working some species are decimated or even wiped out, others are favoured and may develop very great densities. In this way the community may be radically changed but this does not mean that the important process of decomposition of organic remains is necessarily disturbed. Resistant species may take over the function of eradicated ones and in some cases it was reported that insecticide treatment resulted in quicker decomposition. However, the interrelationships within the soil community, including those with microorganisms, are extremely complex and we are at present far from being able to predict the effects of pesticide application with any exactness.
Insecticides may also influence microbiological activities in the soil. Thus Chandra found inhibitory effects of dieldrin and heptachlor on nitrification and microbial numbers, which decreased with higher temperatures and increasing time.
Industrial exhalations may also influence soil communities. Vanek studied the oribatid communities in North Bohemian fir forest and found considerable differences in species composition and total abundance between polluted areas and non-polluted ones. The chlorine content seemed to be the most important cause of the toxicity.

FORCES EVOKED BY SOIL COMMUNITIES

The dynamics of the soil community, subject to forces from outside and exerting forces inside, include finally the forces exercised in the environment. These forces interest man mainly in his attempts to cultivate soils, to improve and maintain soil fertility and to prevent soil erosion.
The effects of soil life on the environment are physical and chemical in nature. Physical influences concern the structural fabric of the soil: formation of conglomerates consisting in a thorough mixture of organic and inorganic substances; construction of galleries of varying sizes, often coated with excreted products; and shifting of organic debris into deeper layers and inorganic materials onto the surface. Though the effects of animal activity are the most apparent, those of microbial life are no less important. Excretion products of bacteria and fungi may considerably influence crumb formation.
Casting by earthworms is one of the most impressive effects of soil fauna activity. It was studied more than a hundred years ago and still it takes its place in the programme of soil biological conferences. Zajonc has studied primarily the seasonal aspects of the deposition and found influences of thawing in spring and rainfall in autumn. In this case, the simultaneous occurrence of leaffall and maximum casting caused the leaves to adhere to the soil, preventing their transport by wind and water.
The chemical activities of the soil community discussed here are those relating to the decomposition process.

A study on the decomposition rate in mull, moder and mor types of broad-leaved forests in the Quebec Region, Canada, was made by Maldague. He reported rather high weight losses of the litter in the first year in each of the three types, mainly attributed to microbial attack. The differences in weight loss - highest in mor, least in mull - are thought to be caused by micro-climatological influences. In the second year, the rates of weight loss were reversed. In the mor this may have been due to the very poor fauna exerting a negligible influence, whereas micro-arthropods in moder and earthworms in mull are active agents in decomposition. The resulting accumulation of organic matter was three times larger in mor than in mull. The comparison with a tropical forest in the Congo is interesting. Here, with a leaf-fall about six times greater than in the Quebec mull site, the accumulated matter in the soil was about the same.

The difference in assailability of organic matter in different horizons in the profile was described by M i n d e r m a n. Oxidizing the organic matter from increasing depths with a mixture of 0.25 N potassium bichromate and 96 % sulphuric acid, he found increasing amounts of residues, pointing to decreasing assailibility at greater depths.
Decomposition of litter results from the combined action of microorganisms and fauna. Both activities are intermingled in an intricate way and in nature it is not possible to separate them completely. Nevertheless it is worthwhile to go into these processes separately. Whereas it seems impossible to exclude microbial activity in faunal studies the exclusion of the fauna, or in any case a substantial reduction of its activity, is less difficult. Thus H a i d e r and S c h e t t e r s have studied the decomposition of lignin in straw by microorganisms and the formation of humic substances. They found phenoloxidase-excreting organisms, which were active cellulose and lignin decomposers and which also produced large amounts of humic substances in pure cultures.
O k a f o r studied the microbial attack of chitin strips in soil. Besides species which were able to clear chitin alone, there were others which only cleared chitin in concert with others. It is supposed that the enzymes necessary for clearing are present in the first, but only partly in the others and that these supplement their deficiency from other organisms.
The microbial decomposition of various litters was approached in very different ways by T s u r u and by H o w a r d. The first author studied the effect of several microorganisms on the composition of the litter, the production of humic substances and the differences in various soils. H o w a r d measured the respiration in litters from various tree species in glass tubes under semi-natural conditions. In most cases there was a pronounced fall in respiration rate during the first 25 weeks, followed by a slower fall or levelling out, caused by a gradual depletion of easily accessible nutrients. By this method it is possible to compare the rate of decomposition of various litters originating from various sites, in different soil types. Though animal influences were neglected in this study, the method is sufficiently adaptable to be used in studies involving small animals too.
V o n T ö r n e did experiments on decomposition of cellulose by several microorganisms combined with various Collembola species. He found only a slight effect of the animals superimposed on the microbial effect. The variation in decomposition rate seemed to be greater in experiments with animals than in those without. Cropping of fungal mycelia by Collembola sometimes resulted in a diminution of the rate of decomposition,

though in experiments of longer duration, the inhibition was counterbalanced by a positive contribution of the animals to the decomposition process.

The role of macrofauna in soil formation was investigated by Szabó, Bártfay and Marton. They found considerable influence of ***Bibio*** larvae colonies in mixed forests. At the estimated density of 200 per m^2, about 15% of the litter was consumed. They recorded the differences in the microflora in litter, gut contents and faeces and found a considerable reduction in the number of species of microorganisms in the intestinal canal. By paper chromatographic analysis they were able to demonstrate that *Streptomyces finlayi*, which is dominant in the intestine but also occurs in litter and fresh excrements, is a main agent in the disappearance of free amino acids in the decomposition of litter. This paper shows clearly an aspect of the interrelationships between an animal species and microorganisms and the effect of their combined action in decomposition.

The relations between microorganisms and fauna and the importance of climatological, microclimatological and edaphic factors on spruce litter decomposition are clearly demonstrated in the paper by Zachariae. High precipitation and nocturnal dew formation in summer create in the upper soil layer favourable humidity conditions for microbial activity. This results in relatively quick decomposition of litter in the soil providing favourable feeding conditions for large tunneling earthworms. Earthworm activity again prevents litter accumulation at the surface as the needles are drawn into the soil by the worms or washed into cracks and galleries by rain. The absence of a closed litter-layer promotes the penetration of cool water-saturated air in the soil pores and condensation on the walls of burrows and cavities. The dynamic interaction between abiotic and biotic factors results in this case in a rather optimal litter decomposition and humification, the ultimate cause of which may be seen in the favourable microclimate in the upper soil.

The effect of fauna and microorganisms on the decomposition process in straw compost with varying amounts of superphosphate was studied by Altemüller and Tietjen. The increasing inhibition of the decomposition with increasing percentages of superphosphate was recorded both by chemical analysis and by microscopic observations of 0.02 mm slides. It is clearly shown that this microscopic investigation provides an excellent means for analysing quantitatively the various stages of disintegration, which to a certain extent the authors could attribute to the acti-

vities of micro- and macro-organisms. It seems certain to me that this technique has promising possibilities for the study of the decomposition process.

Concluding, we see that many aspects of soil biology were put forward around the theme "Dynamics of Soil Communities". New techniques were illustrated, new approaches to old problems were discussed, new problems were raised. Many papers give evidence of a fundamental approach, others originate from practical agricultural problems. In a rather young scientific branch such as soil biology is, fundamental studies are needed to fill up the many gaps in our knowledge. However, contribution to the solution of problems in agricultural practice cannot be postponed. It is encouraging to notice that soil biologists are aware of both needs.